

STEM CASTS OF *LEPTOPHLOEUM AUSTRALE* (MCCOY) WALTON AND THE RESPONSE OF THEIR LEAF-CUSHION BASES TO COMPRESSION

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The distribution patterns of the widths of leaf-cushion bases on the surfaces of *Leptophloeum australe* casts may be used to determine whether they were elliptical or circular in section prior to their compression. Given the outline shape of a cast and its maximum width and length in section the diameter of the original stem can be calculated. □ *Leptophloeum*, cast, leaf-cushion, compression.

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Casts and moulds of *Leptophloeum australe* (McCoy) Walton have been reported from Upper Devonian and Lower Carboniferous fresh-water deposits throughout Laurasia (Anderson & Anderson, 1985; Cai & Wang, 1995; Dawson 1862, McCoy, 1874) and Gondwana except for South America and Antarctica (Edwards & Berry, 1991). The absence of the species from these two continents may merely reflect inadequate collecting because in those times they were closely connected with the remainder of Gondwana (Scotese & McKerrow, 1990).

The casts derive mainly from the infilling of hollow stems whose central tissues decayed leaving only a thin sheath of outer cortex and leaf-cushion bases. The evidence for the stems of *Leptophloeum* being herbaceous is compelling. None of the casts studied taper and none bear the scars of shed branches as do those of *Lepidodendron* (*Ulodendron*); the outlines of the leaf-cushion bases, irrespective of the cast diameter, are all of the same shape and meet along their margins; in contrast the leaf-cushion bases on larger *Lepidodendron* casts are often laterally distended and are more or less separated thereby confirming that they grew out from stems which had experienced secondary growth. Assuming the stems of *Leptophloeum* were herbaceous they may be compared with those of present-day *Agave* spp. which shortly after flowering rapidly decay except for a sheath of encircling leaf-bases. Though *Agave* stems are initially erect and circular in section (Fig. 1) the dying or dead flowering stems soon topple to the ground where, under the influence of gravity, they become elliptical in outline. As a result of the slow decay of the sheathing leaf-bases, with

the passage of time, the minor axis of the ellipse becomes shorter and its major axis longer.

Infilling and burial of the hollow stems of *Leptophloeum australe* results in the formation of internal casts on whose surfaces are imprinted the outlines of the leaf-cushion bases as seen from the centre of the stem (Fig. 2A). Their outlines are rhomboidal and they have concave surfaces (Fig. 2C). Therefore the leaf-cushion impressions on moulds derived from these casts are rhomboidal in outline with convex surfaces. Casts of whole stem segments with details of the stem surfaces preserved thereon are rare and readily distinguished from internal casts. Depending upon the amount of decay experienced by the stem surface, prior to the formation of the cast, the outlines of the leaf-cushion bases are more or less distinct but their surfaces are always convex (Fig. 2B,D). Consequently the surfaces of the leaf-cushion bases on moulds derived from such casts are concave.

By far the majority of casts derive from decaying stems which are aligned parallel to the bedding planes of the host sediments. In section these casts are elliptical in outline with their major axes disposed parallel to the bedding planes and so are presumed to have formed from axes that had toppled over at the site of growth or had been transported to a swamp before infilling. Only two casts with cylindrical sections have been noted. One had eroded from its investing matrix and was collected from a surficial deposit (Queensland Mines Department L1526); the other was erect and preserved in situ (Morris, 1977).



FIG. 1. Erect decaying stem of *Agave vivipara*.

MATERIAL AND METHODS

An internal cast of *Leptophloeum australe* which is elliptical in section and has the pattern of leaf-cushion bases preserved over its whole surface was the starting point for these studies (Clifford, 1996). Assuming, that before burial and compression, the cast was circular in section, the length of its perimeter, was ascertained by multiplying the number of leaves per whorl by the width of the least distorted leaf-cushion base on its surface. Using this length the diameter of the uncompressed stem was calculated. The result revealed that the length of the major axis of the elliptical cast and that of the diameter of the uncompressed circular cast were similar thereby confirming that during compression the width of the cast had not expanded in the plane at right angles to the direction of the applied pressure. Therefore, it can be assumed that when compressed, buried casts suffer little or no lateral expansion. Because the shape and width of leaf-cushion bases in each whorl are similar, their distribution around a circular stem may be expressed as equal arcs on the perimeter of the circle which results from sectioning the stem at right angles to its length. Likewise, the distribution of leaf-cushion bases around the perimeter of the ellipse derived by compression of a circle may also be represented by a series of

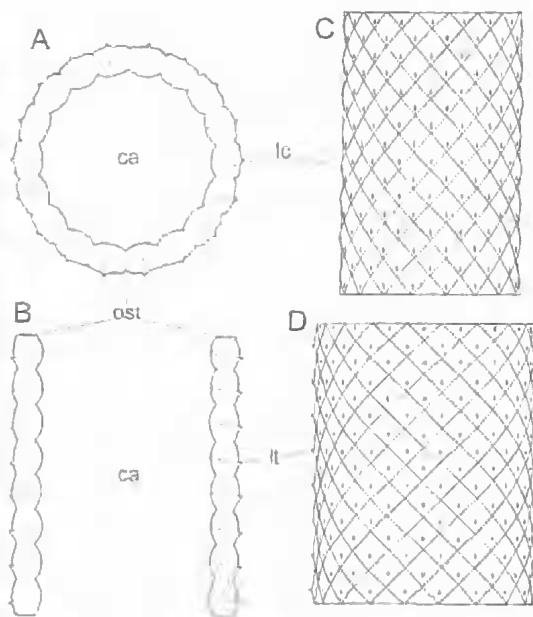


FIG. 2. Diagrammatic view of a decaying stem of *Leptophloeum australe* and two casts derived therefrom; A, transverse section of stem; B, longitudinal section of stem; C, internal cast; D, stem cast. ca, cavity; lc, leaf-cushion; lt, leaf-trace; ost, outer stem tissue.

equal-length arcs. The procedure for determining the co-ordinates which define the margins of the individual leaf-cushion bases around the perimeter of an ellipse is complex. However, with the advent of symbolic manipulators such as Maple, mathematical problems like those encountered in this paper are easily solved. Maple V Release 4 was chosen to furnish these results as described in Appendix 1. Whereas during the compression of a circle into an ellipse the length of its perimeter is conserved, the length of the major axis of the ellipse always exceeds the diameter of the parent circle (Fig. 3).

To explore the responses of leaf-cushion base widths to compression, a circular cast of unit diameter (for practical purposes the unit employed was 100mm) with 32 leaves per whorl was taken as a model. This number of leaves was chosen both because it is close to that observed on the cast previously studied (Clifford, 1966) and is exactly divisible by four thereby giving a whole number per quadrant. The theoretical responses of leaf-cushion bases to compression were investigated for the four uncompressed elliptical and one circular cast whose sections are illustrated in Fig. 3. The perimeters of all sections

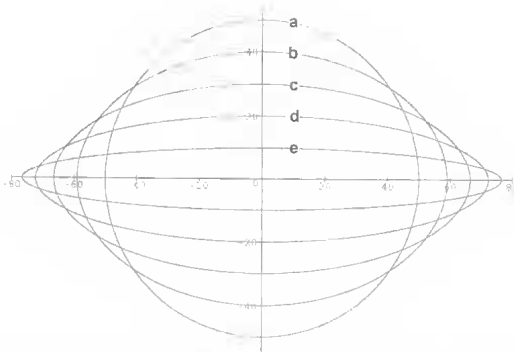


FIG. 3. Circle (a) and four of the ellipses (b-e) which result from its compression.

are of the same length and each bears the same number of evenly distributed equal-sized leaf-cushions. The circular cast was subjected to four levels of compression (Fig. 4) and the elliptical to 3, 2 and 1 level respectively (Fig. 5). The dispositions of the leaf-cushion bases around the perimeters of the sections of the theoretical casts may be calculated as arc lengths but because of the irregularities which occur on cast surfaces it is customary to measure the widths of their leaf-cushion bases in terms of the chord lengths joining their margins. Therefore to permit direct comparisons of the amount of change in the widths of leaf-cushion bases which occurs during compression, chord rather than arc lengths were investigated throughout this study. With theoretical models chord lengths are calculated from the co-ordinates which define the boundaries of the leaf-cushion bases, but on casts the chord lengths are measured directly with a pair of dividers.

RESULTS

The relationships between arc and chord lengths for two leaf-cushion bases from the same whorl about the perimeter of two casts, one of which is circular and the other elliptical in section, are shown in Table 1.

The manner in which the widths of leaf-cushion bases, expressed as chords, vary on the surfaces of theoretical casts of *Leptophloeum* that have been subjected to several levels of compression are given in Table 2 for an initially circular, and in Table 3 for initially elliptical, casts. In both Tables the width of the leaf-cushion bases is expressed as a fraction of that prior to their compression.

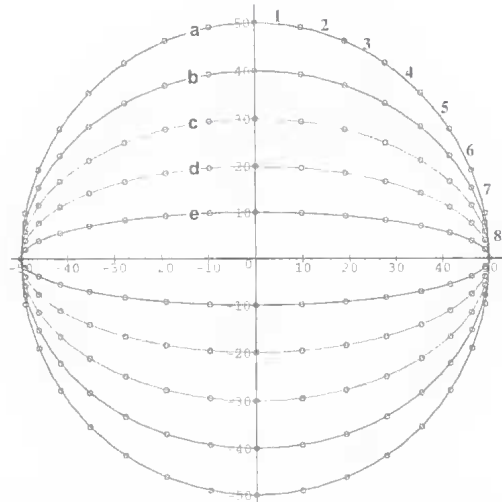


FIG. 4. Circle (a) and four of the ellipses (b-e) which result from its compression subject to the condition that the major axes of the ellipses and the diameter of the circle have of the same length.

DISCUSSION

Whereas for a circle the relationship between chord and arc lengths is constant for leaf-cushion bases arranged around its perimeter, with an ellipse this relationship depends on the position of the leaf-cushion base on its perimeter (Table 1). On surfaces of little curvature arc and chord lengths are similar, but when the curvature is considerable arc lengths are conspicuously longer than chord lengths. Nonetheless, except where the curvature is extreme, the difference between the length of the chord and its associated arc is insufficient for the former not to stand as a surrogate for the latter. Indeed, the greater the compression the more closely the chord length approximates to the arc length on surfaces of minimum compression (Table 1). It is clear from

TABLE 1. Chord lengths expressed as a fraction of their associated arc lengths for two nodes on the perimeters of a circle and those of four ellipses derived therefrom by compression. a-e and 1-8 as in Fig. 4.

Perimeter	Chord length	
	Node 1	Node 8
a	0.99839	0.99839
b	0.99947	0.99486
c	0.99981	0.98393
d	0.99994	0.96106
e	0.99999	0.95799

TABLE 2. Relative widths of leaf-cushion bases expressed as a fraction of their original widths for eight nodes around a quadrant of the perimeters of four elliptical casts derived by compression without lateral expansion of one initially circular in section. b-e and 1-8 as in Fig. 4.

Node no.	Length of minor axis of ellipse as a percentage of the diameter of the parent circle			
	80 (b)	60 (c)	30 (e)	20 (d)
1	1.00	1.00	1.00	1.00
2	0.99	0.97	0.96	0.96
3	0.96	0.92	0.90	0.89
4	0.92	0.86	0.81	0.78
5	0.89	0.79	0.71	0.66
6	0.85	0.71	0.59	0.50
7	0.82	0.64	0.48	0.35
8	0.80	0.61	0.41	0.22

Tables 2 & 3 that irrespective of whether the cast was originally circular or elliptical in section, the widths of leaf-cushion bases, respond in a similar, though not identical, manner to compression.

Furthermore, the amount by which successive leaf-cushion bases differ in width around the perimeter of the cast reflects both its original shape and the amount of compression it has experienced. If the original cast was circular in section a reduction in width by 10% or less is experienced only by those leaf-cushion bases immediately adjacent to the position of minimum curvature on its surface. That is, in proceeding from the position of minimum to that of maximum curvature on the cast surface there is a relatively rapid decrease in leaf-cushion base widths but the amount of decrease between successive nodes is not constant. Close to the positions of greatest and least curvature on the cast surface the difference in the widths of adjacent leaf-cushion bases is less than for pairs of leaves midway between the two (Fig. 6A).

In contrast, if prior to its compression the cast was elliptical in section, a reduction of 10% or less in width is experienced by several, rather than a few of the leaf-cushion bases close to the position of minimum curvature. Furthermore, in progressing from the position of least to greatest curvature on the surface of the cast the differences in the widths of successive leaf-cushion bases increases consistently (Fig. 6B). Therefore, provided they are sufficiently represented, the relative widths of successive leaf-cushion bases in the same whorl offer a reliable guide to the

TABLE 3. Relative chord widths of leaf-cushion bases expressed as a fraction of their original widths for eight leaves disposed around the perimeters of three families of ellipses each resulting from the compression of an ellipse. n-p,r-s and u as in Fig. 5; numbers 1-8 also as labelled in Fig. 5.

Node no.	Minor axis of initial cast/minor axis of compressed cast					
	40/30 (n)	40/20 (o)	40/10 (p)	30/20 (r)	30/10 (s)	20/10 (u)
1	1.00	1.00	1.00	1.00	1.00	1.00
2	0.99	0.99	0.99	1.00	1.00	1.00
3	0.98	0.97	0.96	0.99	0.99	1.00
4	0.96	0.93	0.91	0.98	0.97	0.97
5	0.93	0.87	0.84	0.96	0.94	0.98
6	0.88	0.78	0.71	0.93	0.88	0.96
7	0.81	0.65	0.53	0.85	0.75	0.92
8	0.76	0.52	0.30	0.70	0.45	0.68

cross-sectional shape of the cast before its compression.

GENERAL DISCUSSION

The shape of a cast prior to its compression though of interest, is often of less importance than a knowledge of the length of the diameter of the stem from which it derived. If the leaf-cushion pattern on an elliptical cast indicates it was originally circular in section, then the lengths of its major axis and that of the stem diameter are the same. However, if the pattern of leaf-cushion bases indicates that prior to its compression the cast was elliptical in section, estimation of the diameter of the original axis is more complicated. The complexity arises because two processes are involved. The first of these is the collapse, under the influence of gravity, of the original circular hollow stem into one elliptical in outline before becoming infilled to form a cast; the second is the response of that cast to compression. Because the girdle of leaf-cushion bases encircling the decaying circular stem forms only a narrow band of tissue its collapse under the influence of gravity results in the stem assuming one of an infinite number of elliptical outlines. The length of the major axis of this ellipse is fixed prior to its being infilled to form a cast (Fig. 1). With one exception, the lengths of the major axes do not provide a direct estimate of the size of the original cast. The exception is when the transectional area of the cast approaches zero in which circumstance the length of the perimeter of the ellipse approaches twice that of its major axis. Such ribbon-like casts are abundant and derive from hollow stems which have collapsed completely

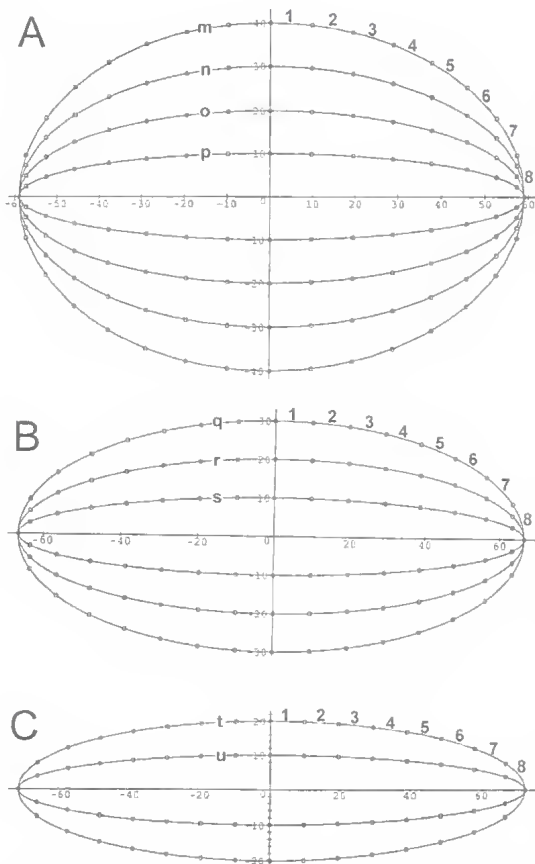


FIG. 5. Ellipses resulting from the compression of three ellipses (b-d of Fig. 4), each subject to the constraint that the length of its major axis is not affected by the compression.

or almost so, before being infilled to form a cast. The surface of such ribbon-like casts corresponds with that of the parent stems and so their leaf-cushion bases have convex surfaces (Fig. 2D).

When the minor axis of the elliptical section is much shorter than its major axis, the perimeter of the original circular stem can still be estimated provided the amount of compression is known. One estimate of this amount is provided by the cast previously reported upon (Clifford, 1996). During compression its cross-sectional area was reduced to 50% of the original. As this cast is typical of all others encountered it has been assumed that they too will have experienced a similar amount of compression. Therefore the lengths of minor axes of casts known to have been elliptical in section before compression will have been reduced by a half although their major axes will not have changed in length. The minor

axis of the uncompressed cast must be twice that of the observed cast, a statement that is confirmed by the following relationship between the area of an ellipse and that of its axes:

$$A = \pi ab$$

where A is the area of the ellipse, a is the length of its semi-major axis, b is the length of the semi-minor axis.

Given the lengths of the semi-major and semi-minor axes of an ellipse the length of its perimeter may be calculated. For high accuracy it would be necessary to use elliptical integrals to resolve the problem but for the present purposes the following approximation is sufficiently accurate:

$$P = \frac{\pi}{3}(a + b + \sqrt{8(a^2 + b^2)})$$

where P is the perimeter, a and b are defined as above.

It should be noted that to determine the perimeter of a cast prior to its compression the value of b to be employed is twice that observed on the compressed cast. The above discussion has assumed that the shape of the cast previous to its compression was determined from a study of the dimensions of the leaf-cushion bases on its surface. However, even if the leaf-cushion pattern is incomplete or absent an estimate of the diameter of the original cast is still possible assuming that during compression about half its volume has been lost. Accepting such loss the shape of a cast which is elliptical in section prior to compression may be determined by comparing the length of twice its minor axis with that of its major axis. If the two lengths are similar the original cast will have been circular in outline; if double the length of the minor axis is less than that of the major axis the original cast will have been elliptical in outline. These results stem from the simple relationship between the area of an ellipse (of which the circle is a special example) and the length of its two axes. Should twice the length of the minor axis exceed the length of the major axis it would follow that the cast had lost less than 50% of its original volume, a situation as yet not encountered. The procedure for determining the diameter of a stem whose cast was elliptical before its compression will now be demonstrated using data from a specimen in the collection of the Australian Museum (F6449). The outline of the cast as seen in transection is shown in Fig. 7 together with some points on the perimeter of the ellipse calculated from its maximum and minimum width. The close

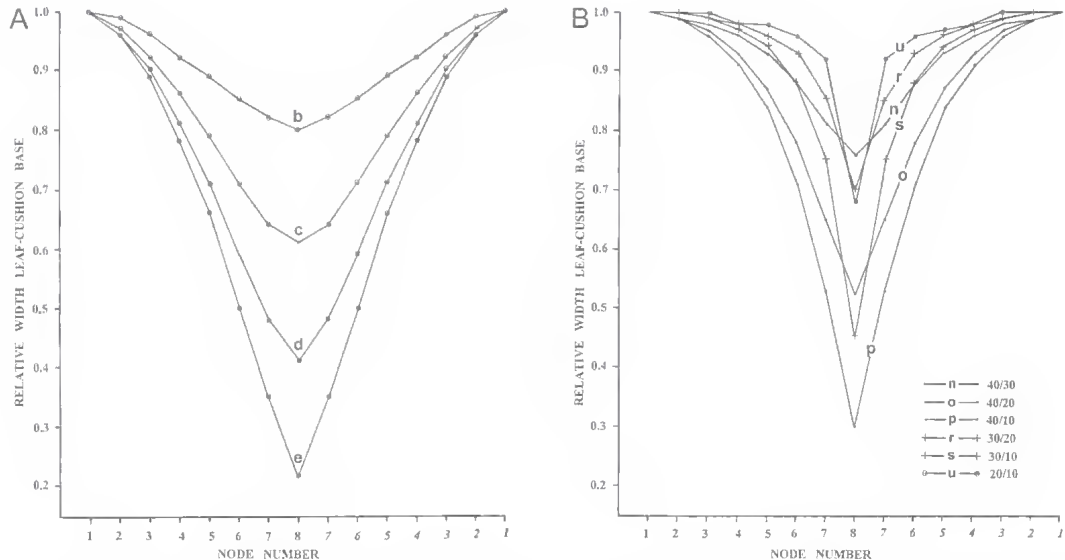


FIG. 6. A. The lengths of the leaf-cushion base widths, expressed as a fraction of their uncompressed value, for 16 leaves arranged around the semi-perimeters of the four ellipses (b-e) illustrated in Fig. 4; B. The lengths of leaf-cushion base widths expressed as a fraction of their uncompressed value for 16 leaves arranged around the semi-perimeters of the ellipses n-p,r-s and u illustrated in Fig. 5; node numbers 1-8 and their mirror images (italics) as in Figs 4 and 5.

agreement between the outline of the cast (Fig. 7, a) and the superimposed points supports the view that the cast arose by deformation of one which was circular in section.

Doubling the length of the minor axis of the ellipse (Fig. 7, a), without altering the length of its major axis results in a new ellipse (Fig. 7, b) which may be taken to represent the transectional outline of the cast prior to its compression. However, as it is postulated that the uncompressed cast arose by the infilling of a circular but hollow stem which had collapsed into an ellipse under the influence of gravity, the length of the perimeter of the uncompressed cast and that of the stem will be the same. The width of the persistent outer stem tissues within which the uncompressed cast is formed may be neglected for it is small compared with the diameter of the cast. The perimeter of the uncompressed cast may be calculated from the formula cited above, and using the result, the diameter determined of a circle with the same length perimeter. This circle (Fig. 7, c) may be taken to represent the outline of the original stem. It should be noted that whereas the transectional area of the compressed cast is only 40% that of the stem it is 50% that of the uncompressed cast. The difference between these two numbers arises because during the deformation of a circle into an ellipse the length of the perimeter is unchanged

but the enclosed area is reduced. Had cast F6449 resulted from the direct compression of a specimen which was circular in section it would have lost c. 80% of its volume. In this circumstance the length of the diameter of the uncompressed cast and that of the major axis of the compressed elliptical cast would have been the same. If such a large loss of volume is acceptable, the width of the uncompressed cast would be intermediate between the length of the major axis of the cast and that of the diameter of a circle derived on the assumption that the hollow stem had collapsed into an ellipse before infilling and then losing 50% of its volume. At present only one cast is known whose surface pattern is sufficiently well preserved to allow its precompression, transectional area to be estimated with confidence. Therefore until further data are available it is necessary to accept that 50% compression of *Leptophloeum* axes is the norm, at least in eastern Australia, and to use this value together with the maximum and minimum widths of casts to calculate their precompression diameters.

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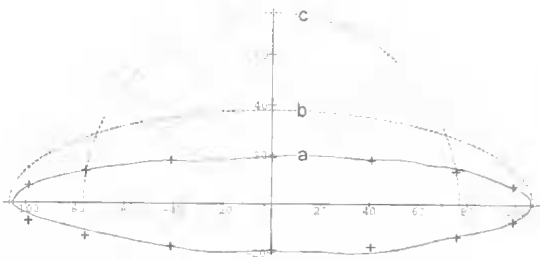


FIG. 7. Outline of an internal cast of *Leptophloeum australe* (Australian Museum F6449) as seen at right angles to its length (a). Points on the perimeter of an ellipse whose major and minor axes are the same lengths as the maximum and minimum widths of the cast (+). Ellipse whose major axis is the same length as that of the cast but twice its area in section (b). Circle with same perimeter as that of ellipse b (c).

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APPENDIX 1

Method of calculation using symbolic manipulator; Maple V Release 4. Maple V Release 3, 4 or 5 can be used for the determination of the various calculations required in this paper and these problems are now discussed in general. Given the circumference of a circle, so that its diameter can be calculated, it is required to find the major and minor axes of ellipses which result from keeping their perimeters fixed as that of the original circle, but whose minor axes are reduced to some fraction of its radius. To find the perimeter of an ellipse it is necessary to calculate an elliptical integral which must be evaluated numerically. In fact, the perimeter is given by:

$$P = 4 \int_0^{\frac{\pi}{2}} \sqrt{a^2 \cos^2 u + b^2 \sin^2 u} du$$

where a and b are the semi-major and semi-minor axes of the ellipse. Maple allows the setting up of this integral in terms of a and b and, once the circumference of the original circle is ascertained, it is possible to calculate the semi-major axes of the ellipses whose semi-minor axes are reduced in a given ratio of their original value (Fig. 3). To do this a numerical method must be set up which starts with an initial approximation to the solution and then uses a steepest descent method to generate closer and closer approximations to the required solution. The degree of accuracy can be chosen as desired. Once the new ellipses have been found the positions of the margins of the leaf-cushion bases must be calculated. Again this must be done numerically. If it is assumed that the leaves are equally spaced around the perimeters of the ellipses then, since the perimeters have been calculated, the arc lengths corresponding to the widths of the leaf-cushion bases are known — it was assumed there were eight leaves per quadrant (see Fig. 4). A similar steepest descent method is now used to step round the perimeter of the ellipse, successively finding the co-ordinates which define the margins of each leaf. This method was also used to produce Tables 2 and 3. Once the co-ordinates of these leaf-margins have been found, those on the contracted ellipses with the same major axes but smaller minor axes are found by merely holding their X co-ordinates constant and decreasing their Y co-ordinates in the appropriate ratios of the required contraction (see Fig. 4). Information on the Maple program can be obtained from M.R. Pemberton at e-mail mrp@maths.uq.edu.au